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Geographic Variation and Hybridization in Populations of Bahama Snails (*Cerion*)¹

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An exceptionally high degree of individual variation occurs not infrequently among natural populations of plants and animals. In such cases it has usually been possible in animals to prove that gene flow from neighboring conspecific populations or selective mechanisms (such as a superior viability of the heterozygotes) are responsible for the maintenance of the variability (e.g., in grasshoppers, *Drosophila*, Coccinellidae). For plants, on the other hand, Anderson (1949) suggests that variability of natural populations is ultimately always due to introgressive hybridization. Introgressive hybridization between sympatric species is not entirely unknown among animals, and a number of cases (e.g., *Bufo*, *Pipilo*, *Passer*, *Terpsiphone*, *Ceyx*, *Vermivora*, *Colias*, fishes) have been described in detail in recent years.

Other cases, suggesting introgression, are more complex and have not yet been fully analyzed. In most of these cases the variability is either due to true introgression (gene exchange between species) or due to gene flow among well-differentiated allopatric populations of the same species. To decide in favor of one or the other alternative is usually difficult, and virtually impossible if the populations involved are on the borderline between subspecies and species. A genus in which many such situations seem to occur is the snail genus *Cerion*, considered "the most difficult genus of pulmonate mollusks to classify" (W. J. Clench, *in litt.*).

¹ Based on work done at the Lerner Marine Laboratory of the American Museum of Natural History, Bimini, Bahama Islands.

THE GENUS *CERION*

This genus has, for a long time, been a challenge to malacologists. Every colony appears somewhat different from every other one. The application of the conventional categories of species and subspecies has been particularly difficult. Although there are now some 600 named entities in this genus, there is no agreement as to the actual number of valid species. The presence of such puzzling variation suggests the existence of special evolutionary mechanisms and aroused among evolutionists an interest in this genus at an early period. Plate (1907) discussed its adaptation, geographic variation, and speciation, and Bartsch (1912-1929) employed it in the course of his experimental studies in the causes of evolutionary change. These earlier studies were, in a sense, premature, not only because they outran the available genetic information, but also because at that time the genus as a whole was taxonomically poorly known. Clench, in a series of recent papers, has greatly added to our knowledge of the species of *Cerion* which occur on many islands of the Bahamas and elsewhere in the West Indies. Yet, in view of the very inadequate knowledge of the relationship of various kinds of *Cerion*, he was forced to employ orthodox criteria and designate most populations with binomials. It was evident from his studies that real progress in our understanding of the nature of species and of populations in *Cerion* could be achieved only through an intensive field and laboratory study of the *Cerion* colonies of a limited area. The Bimini Islands were chosen for this investigation, owing to their convenient location and the manageable size of the area.

ACKNOWLEDGMENTS

The work reported here was done at the Lerner Marine Laboratory at Bimini. The senior author was privileged to stay at the station from March 28 to April 17 in 1952 when the major portion of the material was collected and the habitats were studied. He is deeply indebted to Dr. Charles M. Breder, Jr., for placing the facilities of the station at his disposal, to Mr. and Mrs. Marshall Bishop for assisting the work in manifold ways, and to Pedro Roma, indefatigable, courteous, and well-informed field assistant. Dr. Mont A. Cazier contributed material from South Bimini (locality A) and also from Gun Cay (locality N), an island not visited by Mayr. Mr. Malcolm S. Gordon kindly obtained material from the colonies P₁ and P₂. Dr. William J. Clench made available the unparalleled collections of *Cerion* of the Museum of Comparative Zoölogy, including additional collections from the Cat Cays and from Gun Cay, and assisted this study in every way. He has supplied the description of

Cerion eximium lernerii (Clench, 1956). It was his expert advice which guided the authors throughout. Miss Evelyn Rademacher gave much help in the final phases of completing the manuscript and prepared most of the illustrative material. To all of them the authors are deeply indebted.

OCCURRENCE AND HABITAT

The Bimini group is situated about 100 kilometers east of Miami, Florida, along the eastern edge of the Gulf Stream and along the western edge of the Great Bahama Bank. In addition to the Bimini Islands proper the group includes some islands farther south, of which Gun Cay and North and South Cat Cays are known to be inhabited by *Cerion*. The Bimini Islands proper consist of South Bimini, North Bimini, and East Cay (or East Bimini), together with various smaller mangrove cays (not inhabited by *Cerion*). Vaurie (1952) has given a description of the islands, while Howard (1950) has reported in detail on the ecology of their vegetation.

All the islands are raised coral reef or dunes of coral sand. *Cerion* is usually found only in a rather narrow strip between high-tide line and the edge of heavier vegetation. The individuals of *Cerion* are by no means evenly distributed over the islands. Though *Cerion* is very tolerant of certain conditions (salt spray, desiccation, starvation), it seems equally intolerant of other factors, among which are apparently shade and humidity. As a result, *Cerion* is normally limited to well-defined colonies, each of which is ecologically characterized. A special effort was made to locate every colony in the Bimini group and to get adequate population samples. The location of these colonies is shown on the map (fig. 1). Collecting stations are designated by arbitrary letters (table 1). Additional collections were obtained at two other islands of the Bimini group, Gun Cay and North Cat Cay.

A glance at the map (fig. 1) shows that many areas, which appear suitable for *Cerion*, are not inhabited. Much "*Cerion* country" at the northern tip of North Bimini, for instance, is free of *Cerion*. To ascribe this to the fact that the narrow strip of the island between the outer beach and the inside mangroves is swept by high tides during hurricanes is not entirely convincing in view of the great salt tolerance of *Cerion*.¹ Perhaps,

¹ An experiment on the salt-water resistance of *Cerion* was conducted at the Lerner Marine Laboratory by the senior author with the following results:

March 30, 1952, 9 A.M., beginning of experiment: About 45 South Bimini *Cerion*, from Colony A, were placed between layers of coconut fiber in a glass container of about 2-gallon capacity. The coconut fiber was thoroughly soaked with sea water,

however, these floods wash out of the soil the small algae, lichens, or fungi that are considered to be the principal food of *Cerion*. Fire is completely fatal to *Cerion*, and only dead shells are found in areas recently swept by fire. The south tip of North Bimini (south of Alicetown cemetery), which had formerly a flourishing colony of *Cerion*, had no living specimens in April, 1952, after having been cleared and burned. There were many dead shells in the sand. Likewise, there were no living *Cerion* in the long strip between the Government station in Alicetown and the northernmost houses of Baileytown, an area that had been cleared and burned over and is now more or less densely covered with houses. There are, however, many dead shells and subfossil shells in the sand, indicating the former existence of prosperous populations.

DISPERSAL

"I think you will have to modify your belief about the difficulty of dispersal of land molluscs" (Darwin to Wallace, June 5, 1876).

The fact that many rather isolated islets and reefs are occupied by *Cerion*, as well as the bewildering multitude of "species" on islands such as Eleuthera, Grand Bahama, Cat Island, Great Inagua, and others, indicates great dispersal facility. The Bahamas are an area of annual violent hurricanes during which branches of trees and other pieces of vegetation are blown out to sea. Owing to their extreme resistance to salt water (see p. 3), individuals of *Cerion* disperse readily: "Their distribution is probably entirely by hurricanes or other severe storms, either by drift or even possibly on wind-blown debris. Like other mollusks that live in this general environment, when established they may flourish for a shorter

and several inches of sea water were left standing at bottom of container. Each day all the coconut fiber was thoroughly soaked with fresh sea water.

Twenty-four hours later: Ten snails removed; nine of the 10 crawled around in container after having been washed with fresh water.

April 3: Eleven more snails washed with fresh water; nine of the 11 doing fine 24 hours later. Two were dead, but may have been so at beginning of experiment, as dormant snails were used.

April 5: Seven snails tested; all alive.

April 7: Sixteen remaining snails placed at bottom of glass jar filled to rim with sea water. Four of these removed six hours later and were alive the following morning. Four more snails were removed after 18 hours of submersion; all were alive.

April 12: Remaining eight snails removed from the salt water after five days of complete submergence. Six were dead, but two were still alive.

The experiment shows the tremendous salt-water tolerance of *Cerion*. It is not surprising, therefore, that these snails can get so easily from one island to another. Results of similar experiments by Bartsch (1912) have subsequently come to our attention.

or longer period of time and subsequently be destroyed by storms. Debris from such a storm may move many miles along a coast or even out to sea, later to be cast ashore elsewhere" (Clench and Aguayo, 1952).

POPULATION ECOLOGY

The senior author's acquaintance with living *Cerion* is limited to random observations made during three weeks of collecting. A comprehensive account of the ecology of these snails therefore cannot be given. For more detail, see Bartsch (1920).

ACTIVITY

During the day time, in dry sunny weather, *Cerion* individuals are withdrawn into the shell, attached to a plant stem. Feeding apparently takes place during the night or in rainy weather. Young snails are possibly more susceptible to drying out, as they are more often found near the ground or in dense grass clumps.

FOOD

According to Bartsch (1920) and Jaenicke (1933) food consists of thallophytes and fungi. This would seem to agree with the observation that there is no obvious damage visible on the leaves of the plants on which the snails were collected. On the other hand feces collected from several specimens shipped alive from Bimini proved on analysis, kindly undertaken by Prof. W. H. Weston, Biological Laboratories, Harvard University, to consist entirely of finely comminuted parts of vascular plants. It is possible that these individuals had ingested paper and cardboard from the packing material.

MORTALITY FACTORS

Nothing is known about the enemies of *Cerion* on Bimini. Rats have been reported as killers of *Cerion* on other islands, but no shells were found in any colony in the Bimini group with the kind of damage inflicted by rats (or other vertebrates). However, in some of the snails a small, roundish hole was broken through the shell wall, suggesting attack by some enemy.

At the onset of dry weather the snails crawl upward on trees, shrubs, and grass stalks and outlast long droughts in this position. Shells that have been kept in a dry box for three months are easily revived, and it is said that they can be revived after more than two years (W. J. Clench, oral communication). The complete vulnerability of *Cerion* to brush fires is described above.

The rather general avoidance of woods and moist places by *Cerion* suggests that moulds and other fungal and bacterial diseases are dangerous for them. There is, however, no direct evidence for this assumption. Related and possibly competitive species are absent from these more humid habitats.

Nothing is known about longevity or rate of growth, although there is reason to believe that *Cerion* may become many years old. The fact that less than 30 per cent of the shells appear to be immature, even in prosperous colonies, supports the hypothesis of the longevity of the adults. The crucial period in the life cycle appears to be the juvenal stage.

REPRODUCTION

This presumably takes place during wet weather. After a rainy spell several snails were found (Colony A) about halfway dug into the soil, either feeding or egg laying. The number of offspring per snail is unknown, but in all prosperous colonies there were 20 to 30 per cent young ones. Bartsch writes: "The eggs appear to be deposited at the base of tufts of grass beneath the surface of the ground and, judging from many gatherings of the young in such positions, one is led to believe that a single egg only is deposited at a time. I have never found more than six young (usually 1-4) . . . and these always in different stages of growth, indicating rather long intervals between oviposition" (1920, p. 6). In the same report, Bartsch suggests that it may take from two to three years for the snails to reach reproductive age.

LOCATION OF COLONIES IN THE BIMINI GROUP

A few words should be said about the location of the various colonies on the islands before each colony is described individually (See fig. 1 and table 1 for the location and interpretation of the various colonies.)

EAST BIMINI

Most of the islands of northeastern Bimini are mangrove keys, unsuitable for *Cerion*. However, *Cerion* colonies are found behind the beach of the easternmost, long-stretched island, which is variously referred to as Easter Cay, East Well, or East Bimini. Shells were collected at the southern point (fig. 1, L), and at the northernmost extremity (fig. 1, W) of the island, which is 4.2 kilometers long. A sample (fig. 1, O) collected by Pedro Roma about halfway on the island was also studied by the present authors.

NORTH BIMINI

On North Bimini *Cerion* apparently once had a virtually continuous distribution along a strip facing the outer (western) beaches from the south tip northward to Paradise Point (fig. 1, near B). The rapid spread

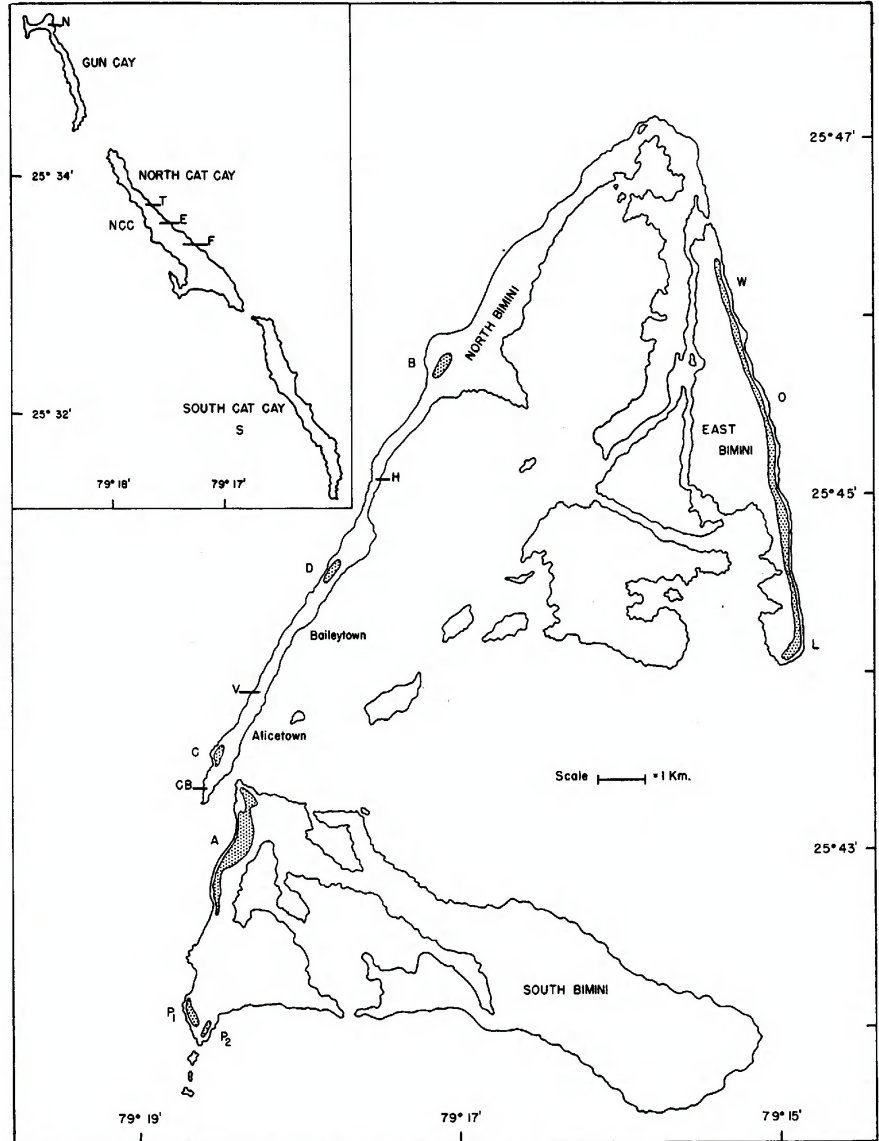


FIG. 1. Map of the Bimini group. Capital letters indicate point of origin of population samples. Shaded area on the main map indicates distribution of living *Cerion* in 1952.

of the villages of Alicetown and Baileytown, as well as extensive planting of casuarinas south of Paradise Point, with burning of grass and brush land, has led to the extinction of *Cerion* on the entire 6-kilometer strip except in three isolated localities (fig. 1, C, D, B). In many areas where the snails have become extinct, it is still possible to pick up dead shells in the sand, some sufficiently bleached and weathered to be described as subfossil (fig. 1, V, H).

SOUTH BIMINI

Most of South Bimini is unsuitable for *Cerion*, because it is covered either by mangrove or by "black earth forest" (Howard, 1950). The only suitable areas occur in the west and southwest. One major colony (fig. 1, A) occurs on sandy soils northwest of the black-earth forest, the other (fig. 1, P) on raised reefs on the southwestern tip of Bimini. Populations A and P are well isolated from each other by a strip of black-earth forest of about $\frac{3}{4}$ kilometer in width.

GUN CAY

Dr. Mont A. Cazier very kindly obtained a large collection from this island (fig. 1, N). The entire series was collected in an area of about 50 feet in diameter at the northeastern tip of the island in a patch of lilies (*Hymenocallis*). Gun Cay is the type locality of *C. pillsburyi* and of subfossil *canonicum* and *northropi*. *Cerion* is evidently very abundant on Gun Cay. Additional samples in the Museum of Comparative Zoölogy were also studied.

NORTH CAT CAY

Cerion were more common on this island than at any other locality visited by Mayr. Furthermore, they showed more ecological variability, ranging from the salt spray zone of reef rocks (fig. 1, E) right into the woods (fig. 1, F). On the northern spur of this island they were common on the trunks of various species of trees (fig. 1, T), i.e., coconut trees and others. They were absent on the southwestern side of the island, beyond the golf course.

SOUTH CAT CAY

One sample (fig. 1, S) was available through the courtesy of Dr. W. J. Clench of the Museum of Comparative Zoölogy.

ECOLOGICAL CHARACTERISTIC OF COLONIES

A short description is given of the ecology and population structure of each colony in the Bimini group. Plant names follow Howard (1950),

the identification being made with the help of a herbarium, prepared by Richard Howard for the Lerner Marine Laboratory. For greater ease of the user, the colonies are listed in the alphabetical sequence of the key letters used in figure 1 and table 1.

COLONY A, SOUTH BIMINI

This, the largest colony in the Bimini group proper, is situated along the northern two-thirds of the west coast of the island. The snails are found in sea oats (*Uniola*) and in shrubbery, particular on "sage"

TABLE 1
LIST OF POPULATION SAMPLES

Arranged geographically (from north to south)

North Bimini: B, D, C; subfossil: H, V

East Bimini: W, O, L

South Bimini: A, P₁, P₂

Gun Cay: N

North Cat Cay: T, E, F

Additional material examined (M.C.Z.)

North Bimini: CB

North Cat Cay: NCC

South Cat Cay: S

Arranged morphologically

biminiense type: P₁, P₂, C, CB

Cat Cay type: E, T, F, NCC, S, (W)

lernerii type: L, D, H, B

Intermediate types: O, V

Hybrid populations: A, N

(*Salmea*) and in palmettos. The colony extends from the northernmost tip (opposite North Bimini) south for about 1½ kilometers to the middle of the island, where the black-earth vegetation reaches the beach and squeezes out the *Cerion* habitat.

A rough census was made of this colony by pacing out the length and width of various rectangles which included all the area occupied by *Cerion*. The area of the colony was roughly determined as being 130,000 square meters. Unfortunately for an exact census the density is very uneven. In six test plots of 25 square meters each, the numbers of snails were 10, 14, 46, 74, 132, and 204. If the frequency of the densest plot were taken to be standard for the whole colony, it would have 1.060800 snails; if that of the plot with the lowest density, 52,000. Because within the 130,000 square meters of the colony there are many areas without any snails and throughout the colony the lower densities are more typical

than the high ones, an estimate of about 50,000 to 100,000 will probably come close to the true population size. In parts of the area the density is very high. For instance, in a single tuft of beach oats, selected at random, Mayr found 27 adults and about one dozen immatures, and this was not an exceptional plant.

In view of the large size of this colony, there is considerable habitat variation within it. *Salmea* bushes, beach oats, and palmettos are, however, found wherever there are snails. There are no snails in the grass immediately adjacent to the beach, the snail belt beginning about 5 to 15 feet farther inland. The width of the colony fluctuates greatly along the 1½-kilometer long stretch. In the south it is only 30 to 50 meters, in the north, 70 to 100 meters, while in the central portion (north of the "well") it extends for about 180 meters from the beach, right to the edge of the mangrove zone of the interior. Although the distribution throughout this wide area is virtually continuous, there is little doubt that this colony actually consists of many sub-colonies differing genetically to a greater or lesser extent.

Colony A is separated from Colony C by the channel between South and North Bimini, and from Colony P by a belt of black-earth forest.

COLONY B, NORTH BIMINI

This area is not more than 120 meters long and 30 meters wide on the Van Campen Heilner property, directly south of the new Lyons residence on Paradise Point. The colony is on a sandy hill between beach and mangroves. Most snails are on *Uniola* grass or on low herbiage, in part under a few *Casuarina* trees. There are virtually no shells on bushes. The colony is small, consisting apparently of fewer than 1000 individuals. Presumably it was formerly continuous with the colony represented by sample D, as there are scattered dead shells throughout the Lyons' property connecting the two colonies. Clearing, burning, and planting of *Casuarina* trees have led apparently to the virtual extermination of the snails.

COLONY C, NORTH BIMINI

This area is now restricted to a stretch of about 200 meters from the Alicetown cemetery northward along the western edge of North Bimini to about 30 meters beyond the foundations of the burned "old hotel." The snails are scanty in this area. Most snails were on bushes, such as *Salmea petroboides*, some on grass (*Distichilis spicata*). The colony is in an area of raised reef rock, bordered in the east by a swampy, brackish area behind the "Airport." The total living population in 1952 probably did not exceed 500 individuals.

Adjacent, to the south, between the Alicetown cemetery and the southern tip of North Bimini, is a stretch of land, about 100 meters long, in which there was formerly a flourishing colony of snails (apparently identical with those now found at C). This is the type locality of *Cerion biminense* Henderson and Clapp (1913). Clearing and burning have destroyed this colony. Many dead shells can still be found in the sand. A sample (CB) from this area was available through the courtesy of the Museum of Comparative Zoölogy.

COLONY D, NORTH BIMINI

This sample represents a flourishing and very populous colony at the north end of Baileytown, just south of the Baileytown cemetery. The colony occupies an open sandy plain (with a few low dunes) behind the western beach and extends at least 200 meters inland. Snails are common in grass, low herbiage, and bushes. The colony appeared healthy and contained many young individuals. It had obviously not been burned over recently. The population size was estimated as 5000 to 15,000 individuals.

COLONY E, NORTH CAT CAY

The sample was taken from the eastern shore of North Cat Cay, about 1.2 kilometers north of the main dock. Snails were very common in this area. Two hundred and fifty adults were picked up in an area 10 meters wide and about 30 meters long. Snails occurred almost down to the high-water line on very dry and scraggly plants. They were found not only on sea oats (*Uniola*), but on various other plants, such as "wild thyme" (*Rachicallis americana*) on which *Cerion* does not occur on North or South Bimini. Colony E is not an isolated colony but a sample from a continuous population extending to the south, west, and north. About 300 meters to the north the colony was sampled at T where the species was equally common.

COLONY F, NORTH CAT CAY

This sample was taken in the center of the island near the northeast end of the golf course. The most remarkable aspect of this colony was that it was found inside dense woods. This is the only locality in the Bimini group where *Cerion* was found inside the forest. The snails were rather scarce at this locality.

COLONY H, NORTH BIMINI

This is a small sample of dead shells picked up at several points in a *Casuarina* grove about halfway between populations B and D. There

were no live shells in this area. The distance between B and D is about $1\frac{1}{2}$ kilometers.

COLONY L, EAST BIMINI

At the southern tip of East Bimini *Cerion* is extremely abundant. The snails are found in a narrow zone, which is only about 50 meters wide, although a few scattered ones go another 100 or 150 meters inland to the edge of salt flats bordering the mangroves. The habitat is somewhat different from that on North Bimini: there is relatively little sand on a rock base. Grass is scarce, and what little there is, is largely *Distichilis* rather than *Uniola*. *Salmea* is rare, and many of the snails are on *Ernodea littoralis* (Rubiaceae), a low-spreading shrub which is more or less avoided by *Cerion* at the other localities.

COLONY N, GUN CAY

This sample in the American Museum of Natural History, New York, was collected by Cazier near the northern tip of the island. No ecological information is available beyond the fact that the snails were collected in a patch of lilies (*Hymenocallis*).

Additional samples from Gun Cay in the collections of the Museum of Comparative Zoölogy were also examined. The letter N in tables and figures refers, however, always to the original sample in the American Museum of Natural History.

COLONY NCC

This sample came from North Cat Cay and is in the Museum of Comparative Zoölogy. It was collected southward not far from Colonies E and T, near the dock.

COLONY O, EAST BIMINI

The sample was collected by Pedro Roma in the middle of the island, about halfway between Colonies L and W.

COLONY P₁ AND COLONY P₂, SOUTH BIMINI

These two samples were taken on either side of the southwestern tip of the island. One sample (P₂) was collected on the shore of Nixon Harbor, the other on the Gulf Stream side of the tip, on the bluff (P₁) about 200 meters north of southern point. Both were kindly collected for us by Mr. Malcolm S. Gordon.

COLONY S, SOUTH CAT CAY

A sample from the collections of the Museum of Comparative Zoölogy was taken at Cat Point, 200 yards north of the south end, and is the only one available from this island.

COLONY T, NORTH CAT CAY

A sample was taken about 300 meters north of Colony E. All specimens were taken from the trunks of five trees (up to 6 feet) which were in the middle of the island in an open grove of trees. The 128 individuals collected were not all of the individuals on the five mentioned trees. Hundreds of other trees were equally covered with snails, and there were many others in the low vegetation. There was no break between E and T, and the colony continued towards the north. The total population on North Cat Cay must number in the millions.

COLONY V, NORTH BIMINI

Dead shells were picked up on the grounds of the Lerner Marine Laboratory. The Laboratory is between C and B, but closer to C (fig. 1).

COLONY W, EAST BIMINI

At the northern end of the island a very scanty population occurs on the dunes behind the beach on "sage" (*Salmea*) and beach oats (*Uniola*). In a stretch of about 800 meters only 10 live and one dead snail were found. This rarity of *Cerion* in this otherwise apparently suitable locality is the more puzzling because the snails are very common and ecologically diversified at the southern tip of the same island (L), only about 4 kilometers to the south. The fact that Pedro Roma was able to gather a fine population sample at the mid-point of the island (O) indicates that the low population density holds true only for the northernmost part of East Bimini.

ECOLOGICAL POPULATION DIFFERENCES

HABITAT

In spite of the essential similarity of the Bimini Islands, there are rather surprising differences in the ecology of the various colonies. Colonies W, D, B, H, and A occur primarily on sand dunes, and L, C, P, and E on outcroppings of reef rock. Most of the colonies are in very open terrain with scanty vegetation, but T lives in a tree grove and F inside a dark forest.

The preference for plants was very different from colony to colony. Trees, including coconut trees, were favored on North Cat Cay, while not a single snail was found on a tree on any island of Bimini proper. In Colonies A, D, and some others, sea oats (*Uniola*) was one of the favorite plants, while C and L preferred another species of grass (*Distichlis*). On East Bimini (L) many snails were found on *Ernodea* and on North Cat Cay (E) on *Rachicallis*, two plants that were neglected in many other areas in favor of *Salmea* or palmettos. As the snails occur at any one locality usually on at least three different species of plants, it seems unlikely that these differences between populations are all due to conditioning. Rather it is to be suspected that the local gene complexes

TABLE 2
THE HABITATS OF BIMINI *Cerion* COLONIES

	<i>lernerii</i> Type	Cat Cay Type	"Hybrid" Colonies	<i>biminiense</i> Type
Reef rock rather bare	—	E	—	—
Reef rock with vegeta- tion and sand	L, (O)	E, (O)	N ^a	P, C, V
Sand dunes	(W), B, H, D	(W)	A	—
Open shrub and grass country	D	T	A, N ^a	—
Open tree groves	—	T	—	—
Inside forest	—	F	—	—

^a Habitat not quite certain.

lead not only to differences in morphology but also to those of habitat and food preference. A glance at table 2 shows at once that the population of North Cat Cay, which is the most populous colony investigated during this study, is also ecologically the most diversified. It occurs in all possible habitat types, including some (coral rock, trees, forest) not occupied on the other islands. The ecology of the Gun Cay and South Cat Cay populations was not studied.

POPULATION SIZE

All levels of population size were encountered. Colony C is an isolated colony of fewer than a thousand and possibly fewer than 500 individuals.

In the area of W only 10 live snails (and one dead one) could be found along a stretch of about 800 meters during a search of several hours. Colony B, as it now exists, counts apparently fewer than 500 individuals. Colonies P and D are medium-sized colonies, while A, N, L, and Cat Cay are very populous colonies, of the order of magnitude of 100,000 individuals and more. Within the large continuous colonies there is good evidence for heterogeneity. For instance Colonies E, T, and F on North Cat Cay are members of a continuous series of populations.

VARIABLE CHARACTERS

The genus *Cerion* seems to be one of those instances where the application of specific and subspecific names to population samples has perhaps hindered more than facilitated an understanding of variation and evolution. The taxonomy of this group is still largely on the "alpha level" (Mayr, Linsley, and Usinger, 1953), and few serious attempts have been made to group related populations into species complexes or polytypic species. A notable exception, and the beginning of a new phase in *Cerion* systematics, is Clench and Aguayo's (1952) revision of the *Cerion scalarinum* species complex. The reasons for the reluctance of students to recognize polytypic species will become apparent in the following two sections. In view of these taxonomic difficulties it would seem best to lay a solid foundation for discussion by an analysis of the variation of characters, rather than of "species" or "subspecies." This procedure has several advantages. It is strictly objective and avoids the bias often introduced by the application of taxonomic names. It provides the necessary information for the eventual taxonomic classification, and finally it permits a study of the factors that affect the geographic variation of populations. These factors include dispersal versus isolation of the populations from one another and the possible selective effect of different environments. If the geographical variation of habitat selection, which is treated in the preceding section, and the variation of the internal anatomy, which is insufficiently studied, be left aside, known variation concerns principally the shell. Here four groups of characters can be distinguished—size, proportions, sculpture, and coloration. Each of these again can be subdivided into more specific characters. Sculpture, for instance, includes size of columnar and parietal teeth, shape of peristome, presence or absence of costation, size of ribs, number of ribs per whorl, number of whorls, and so forth. Among the many characters used to distinguish various species of *Cerion* are some that do not seem to vary appreciably among the 19 studied population samples of the Bimini group. These are:

Shape of shell aperture
Shape of peristome
Size of peristome
Size of parietal tooth
Size of columnellar tooth
Structure of umbilicus
Structure of embryonal whorls
Shape of apex

Several of these characters have been used in published descriptions of Bimini *Cerion* as well as in the standard handbook of Tryon (Pilsbry, 1901–1902), but the present authors were unable to discover significant population differences in these characters in the Bimini group. A thorough discussion of the remaining characters will help to understand the relation of the various colonies to one another.

All measurements are stated in millimeters.

LENGTH

Length refers to the maximal dimension and was measured from the tip of the shell to the lowest point of the lip. Only fully adult individuals were measured. A measurement from the tip to the base of the spine might represent the actual size of the shell even better, but is difficult to take accurately, because the last whorl often slopes considerably and is not well set off against the lip.

A glance at figure 2 shows that one population (F), with a mean length of 21.34 ± 0.56 is considerably smaller than all others. The shells of 12 samples are of medium size (mean within the range, 23–26 mm.; O, W, V, C, CB, C, P₁, P₂, E, T, N, and S). Finally five samples (L, B, D, N, A) consist of large shells (mean 26.31 ± 0.10 to 29.41 ± 0.15).

VARIABILITY: The degree of variability is remarkably similar in most samples, the coefficient of variability (C.V.) fluctuating between 5 and 7. The few exceptions are either very small lots (F, W) or heterogeneous samples (H). This similarity in C.V. for length between the "hybrid populations" A and N (see below) and the otherwise very uniform populations E, T, and P, is partly caused by the presence of a few giants in these latter samples. One or two exceptionally large individuals occur also in L, H, D, V, C, S, A, and N. These samples do not form normal curves. For instance, all specimens of P₁ measure 21.8–25.9, except for one that measured 27.4; all T measure 20.9–27.4, except for two individuals (28.4, 33.4) (fig. 8). Such exceptionally large individuals have been described (e.g., Boettger, 1952) for many genera of mollusks and have been ascribed in some instances to a destruction of the gonads by parasites or to other pathological processes.

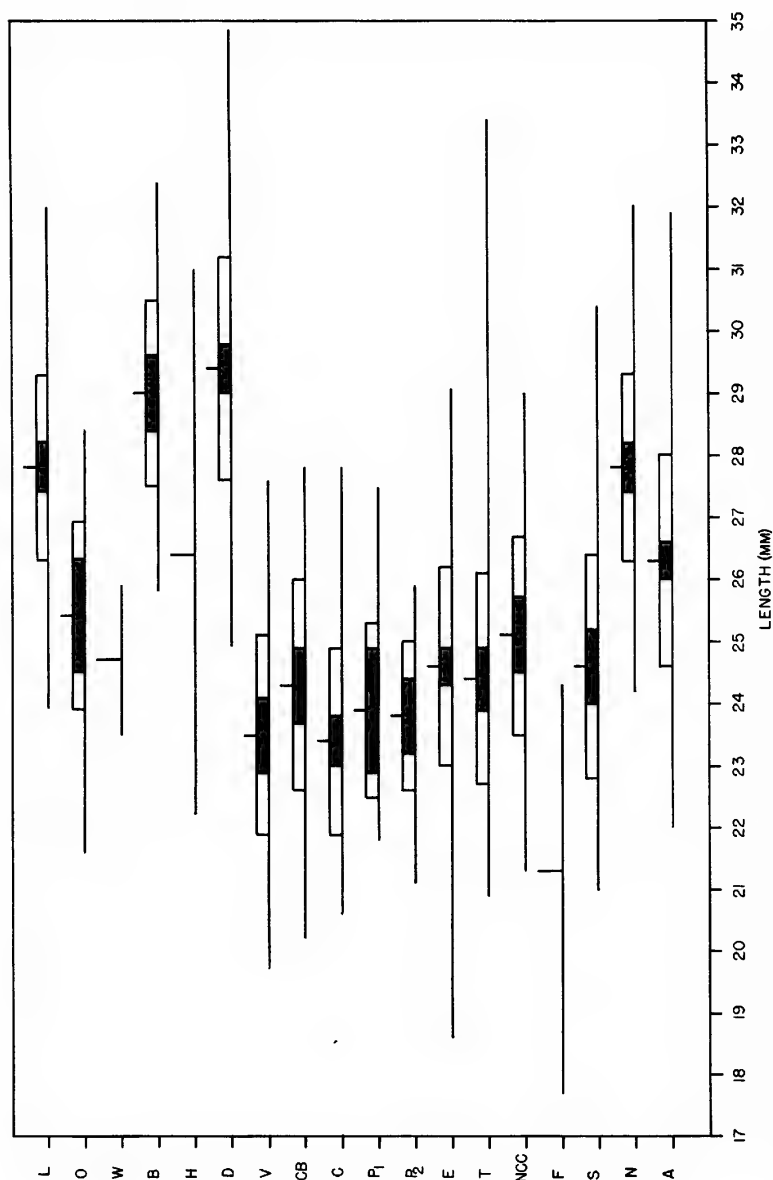


FIG. 2. Statistics of shell length in 18 population samples. Based on the Hubbs and Hubbs (1953) modification of the Dice and Leraas method of graphic representation. The black rectangle corresponds to $3 \times S.E.$; the open rectangle, to $1 \times S.D.$.

As noteworthy as the high variability of some "pure" colonies is the low *C.V.* in two populations (A, N) which on the basis of their exceedingly high variability in color and sculpture are believed to be of hybrid origin. The *C.V.* is 6.42 for A and 5.25 for N, as against 6.58 for E, 6.83 for T, and 5.98 for P₁. Size is presumably determined by a much greater number of genes than either sculpture or color. It is to be expected that hybridization will affect the variance of a highly polygenic character less than that of an oligogenic trait. It is also possible that size is exposed to

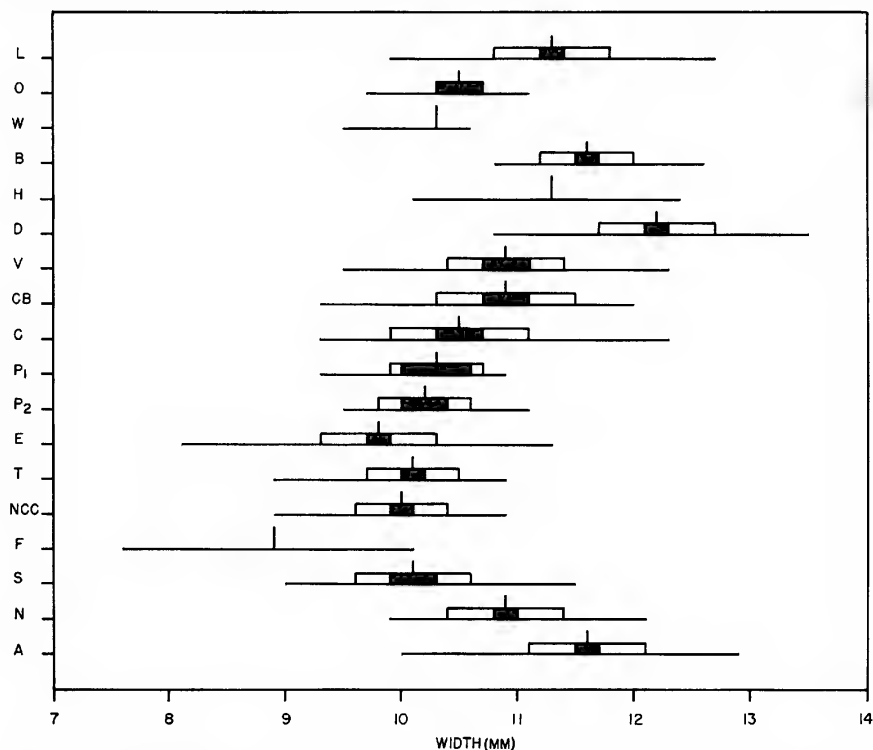


FIG. 3. Statistics of shell width in 18 population samples. Based on Hubbs and Hubbs (1953) modification of Dice and Leraas method of graphic representation. Black rectangle corresponds to $3 \times S.E.$; open rectangle, to $1 \times S.D.$ higher selection pressure than either coloration or sculpture and that a polygenic character may respond to selection more readily. In the case of unmixed and mixed human populations, Trevor (1953) found likewise no differences in metric characteristics.

WIDTH

Width is measured as the greatest diameter at right angles to the length of the shell. If shells from all localities had the same shape, width would

be a simple function of length, and the sequence of population means for width (fig. 3) would run parallel to the sequence for length (fig. 2). This is not the case, which proves that there are differences in shape between colonies: the smallest absolute width is found in the Cat Cay colonies (F, T, E, etc.), slightly greater width in the O, W, C, P colonies, and the greatest width in A, L, B, and D.

VARIABILITY: Width is a much less variable statistic in adult *Cerion* than is length. The *C.V.* for width is smaller than that for length in every one of the examined samples, the average difference for all samples being 1.58, ranging from 0.06 to 4.21. *C.V.* is below 4.0 in P₂ (3.53), T (3.95), S (3.90), B (3.88), and W (3.70); it is between 4.0 and 4.99 in P₁, N, A, D (4.03), and L. It is above 5 in C (5.7), E (5.01), and H (5.05), and it rises above 5.7 in only one small sample, F (8.29). Again it is remarkable how low the *C.V.* is for the "hybrid" populations A (4.55) and N (4.30). There is a slight tendency for very oval shells (C) to have an increased variability in the width of the shell.

GENERAL SHAPE

Two extremes in shell shape are found in Bimini *Cerion*: cylindrical and oval. In a *cylindrical* shell, the full width is reached within a few whorls from the apex and the remaining whorls are virtually of the same size so that the lateral contour of the shell seems to be formed by two parallel lines. In an *oval* shell also there is a rapid increase in size of the early whorls, but this increase tapers off only slowly. Sometimes the last whorl or the two last whorls appear (they really are not!) to be smaller than the preceding ones. This impression is enhanced by the fact that the last whorl may taper towards the shell mouth.

No practical way was found by which to measure these differences in shape. On the whole, however, the most oval shells are the relatively widest ones and the most cylindrical the relatively narrowest. The relative width of the shell (that is, the greatest width expressed as per cent of the greatest length, or W/L index) thus can be used as an approximate measure of shell shape.

WIDTH/LENGTH INDEX: This is obviously lowest in some of the highly cylindrical shells of T (32.0); it is highest in some of the individuals of hybrid population A (up to 55.2) but hardly less in some individuals of C (up to 52.5). The highest mean value is found in V (table 3). The average *C.V.* for the 16 samples is 5.66, which is considerably more than the average of 4.75 for the *C.V.* of width of these same samples. This index is thus a statistic that shows a good deal of individual variability within each sample.

SHELL MOUTH: The size of the shell mouth is very closely correlated to the width of the shell, varying between 91 and 97 per cent of the width.

SIZE AND SHAPE: It has been contended that larger snails tend to be more elongated, smaller ones most compact. There is no evidence for this among the Bimini *Cerion*. Small-sized colonies (F), medium-sized colonies (T, W, O), and large-sized colonies (D) have a very similar width/length index.

TABLE 3
RELATIVE WIDTH ($W \times 100/L$) OF *Cerion* OF THE BIMINI GROUP

Population Sample	Mean	Range
N	39.41	33.9-46.3
NCC	39.92	34.6-45.5
B	40.11	35.1-46.3
L	40.59	35.3-46.3
E	40.625	35.2-47.8
W	41.03	38.4-43.1
S	41.14	35.9-47.3
D	41.50	36.1-50.0
T	41.695	32.0-48.0
O	41.78	36.4-45.5
F	41.96	38.2-44.3
H	42.76	41.0-48.6
P ₂	42.95	40.1-46.4
P ₁	43.41	38.7-50.0
A	44.41	36.5-55.2
CB	45.00	41.1-52.2
C	45.03	39.6-52.4
V	46.60	39.4-52.4

It is to be noted, however, that related colonies cluster together (fig. 4). The colonies of the Cat Cay group (F, T, S, E, NCC) are small and rather slender, the colonies of the *lernerii* group (D, L, B) are large but also comparatively slender, while the colonies of the *biminiense* group (C, CB, P) are distinctly wider. The two subfossil samples (V, H) and the two hybrid colonies (A, N) fall outside the areas of the other samples.

SCULPTURE

COSTATION: The most conspicuous feature of sculpture in these snails is the presence or absence of ribs. The term "sculpture" in this discussion refers to the degree of costation. Costation is, however, not an "all or

none" character. The two or three apical (embryonic) whorls are smooth even in the most heavily ribbed snails. Inversely, even "smooth" snails generally have some ribbing on the last whorl. To achieve more precision, an arbitrary scale of "sculpture" was devised, ranging from 0 (even last whorl without ribs) to 4 (most heavily ribbed shells). If there are regular ribs on the back wall of the shell mouth the rating 0.2–0.3 is given; if there are regular ribs on the last whorl directly above the parietal callus,

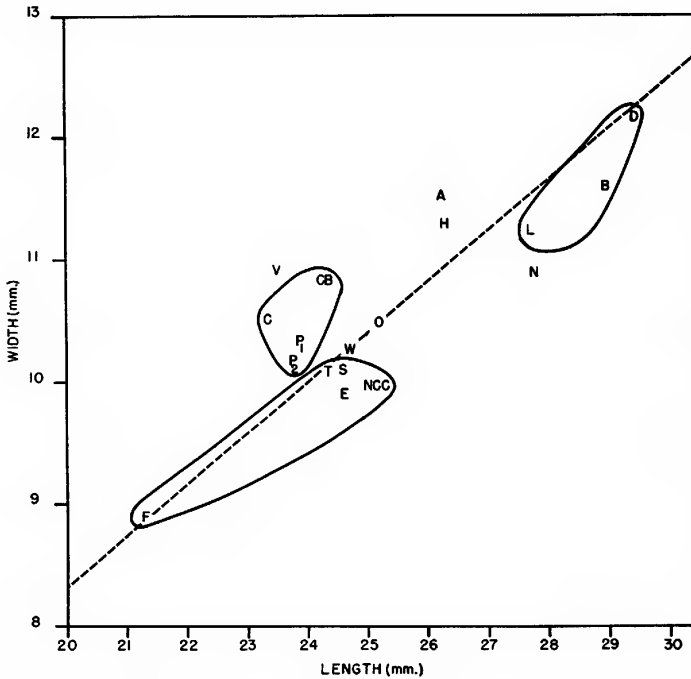


FIG. 4. Scatter diagram of population means of length versus width. Cat Cay group (F, T, E, S, NCC), *biminiense* group (C, CB, P), and *leneri* group (L, B, D) encircled. Dotted line indicates width/length index of 41.5.

the rating is 0.4–0.5. If there are fairly regular ribs on the penultimate whorl (but not regular enough for a count to be made) the rating is 0.6–0.9. If the ribs can be easily counted on the penultimate whorl a rating of 1–4 is given, depending on the degree of heaviness of the sculpture. This rating is highly subjective, and the eventual analysis of the data indicated that it might have been more revealing if the grades 0–3 had been given to the smooth and irregularly ribbed shells (here ranked 0–0.9), and 4 and 5 to the regularly ribbed shells (here ranked 1–4). Regardless of any rating, however, the data bring out clearly various facts (see table 4 and fig. 5).

There are a number of populations, namely, southern North Bimini (C), southern South Bimini (P), and North Cat Cay (E, T) which are consistently heavily ribbed, with relatively low variability. Interestingly enough an unribbed specimen may occur as an exception in such populations. There is one such specimen (0.0) in population F from North Cat Cay and another one (0.4) among 68 CB specimens (M.C.Z. collection). In the case of the North Cat Cay population F, in particular, it is obvious that genuine polymorphism is involved, not hybridization with a smooth-shelled population, because there is no smooth-shelled population on the island.

TABLE 4
FREQUENCY OF SCULPTURE CLASSES (SEE TEXT)

	0	0.1-0.2	0.3-0.4	0.5-0.6	0.7-0.8	0.9-1.0	1.1-1.2	1.3-1.4	1.5-1.6	1.7-1.8	1.9-2.0	2.1-2.2	2.3-2.4	2.5-2.6	2.7-2.8	2.9-3.0	3.1-3.2	3.3-3.4	3.5-3.6	3.7-3.8	3.9-4.0	N
L	61	41	23	14	6	1	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	148
O	—	—	1	4	4	11	3	—	1	1	2	—	—	2	2	—	2	—	1	—	—	34
W	—	—	—	—	—	—	—	—	2	1	—	—	—	—	1	1	—	1	—	1	1	8
B	10	29	11	9	1	2	1	—	3	—	2	—	—	—	—	—	—	—	—	—	—	68
H	1	3	2	4	2	1	—	—	2	—	1	—	—	—	—	—	—	—	—	—	—	16
D	4	4	23	33	30	29	10	—	10	3	5	3	—	—	—	—	1	—	—	—	—	155
V	—	8	26	19	11	—	1	—	1	—	—	—	1	—	—	—	—	—	—	—	—	67
C	—	—	—	—	—	—	—	—	—	1	2	1	—	12	20	60	—	2	1	—	—	99
CB	—	—	1	—	—	—	—	—	—	—	2	4	—	8	7	20	16	—	9	1	—	68
P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	17	19
P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	5	5	8	13	34
E	—	—	—	—	—	—	—	—	3	6	10	6	1	9	9	84	53	2	32	17	12	244
T	—	—	—	—	—	—	—	—	—	1	1	—	—	2	10	34	37	1	18	4	2	110
NCC	—	—	—	—	—	—	—	—	1	4	3	7	—	9	14	13	15	—	6	—	—	72
F	1	—	—	—	—	—	—	—	—	—	—	1	—	1	2	2	4	—	2	1	—	14
S	—	—	2	1	—	1	2	—	—	2	3	1	—	8	9	25	10	—	6	6	7	83
N	—	—	6	12	4	3	—	—	—	—	—	—	—	—	18	28	—	17	19	18	19	144
A	1	5	9	11	29	26	2	—	8	4	5	1	2	8	11	57	46	13	17	7	18	280

There is one population (L) that is consistently smooth, with only two individuals having a rating of slightly more than 1 (1.8, 1.1). Most other populations are not merely highly variable, but actually seem to contain two types of individuals; one type is clearly more or less smooth (rating less than 1) and the other is clearly ribbed. Particularly instructive is the increase in ribbing in the geographic series of populations from the vir-

tually smooth population B (91.2% smooth) through H (87.5%) to D (74.3%).

A similar gradient possibly exists on East Bimini where the northernmost population W is 100 per cent ribbed, O is 47 per cent smooth, while L, $4\frac{1}{2}$ kilometers farther south of W, is almost completely smooth (98.5%).

There can be little doubt that the highly variable populations, particularly A and N, are hybrid flocks, and that B, H, and D show evidence of

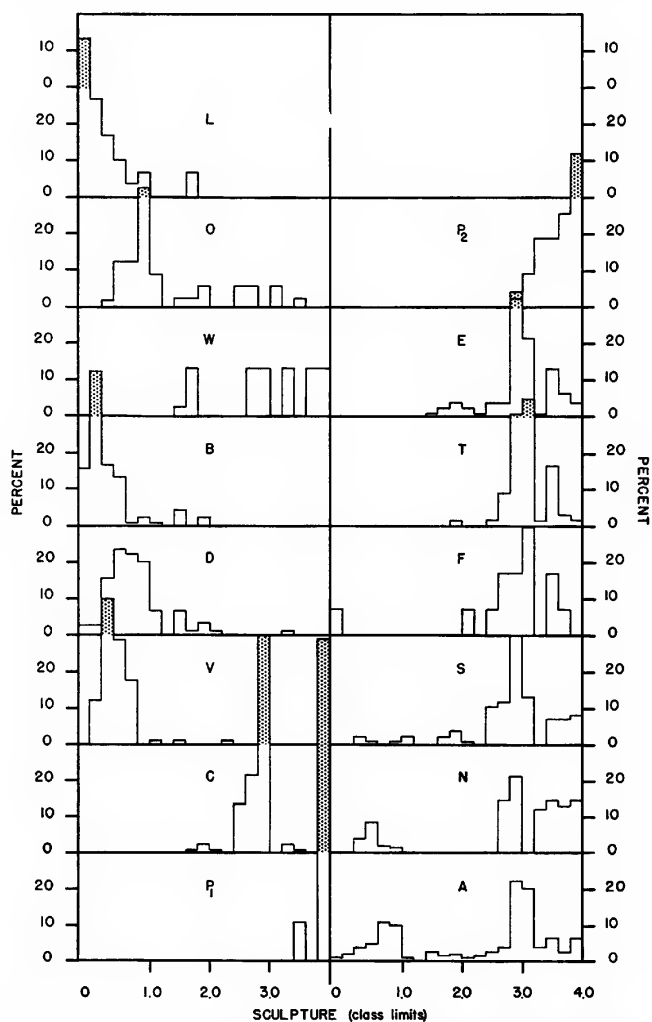


FIG. 5. Histograms of percentage of sculpture types in 15 population samples. Based on data in table 4. Shaded portions indicate percentages above 30 per cent (overlapping other samples).

gene flow from the ribbed population C. Sculpture appears in the populations of *Cerion* to be a much more sensitive indication of gene flow or hybridization than dimensions. The curves for sculpture in the more variable populations are distinctly bimodal, so that it is not meaningful to calculate coefficients of variability.

NUMBER OF RIBS (TABLE 5) : The ribs are counted on the penultimate whorls, from the inner corner of the peristome until one turn of the shell has been completed. This number can, of course, be determined only in those shells in which there is sufficient costation (rating above 0.9).

TABLE 5

NUMBER OF RIBS OF INDIVIDUALS WITH SCULPTURE RATING OF 1.0 OR HIGHER

Population Sample	<i>N</i>	Mean	Range
L	2	(30.50) ^a	26, 35
O	14	(29.00)	24-35
W	8	(26.75)	24-31
B	5	(32.80)	28-36
H	3	(30.33)	26-34
D	41	31.24	27-37
C	99	32.10	24-39
CB	67	34.90	29-43
P ₁	19	30.37	26-36
P ₂	34	31.21	26-37
E	244	26.81	20-35
T	110	27.86	24-35
NCC	72	27.04	21-34
F	13	(30.23)	26-36
S	79	24.89	19-31
N	119	28.24	22-37
A	208	31.80	26-42

^a Means of samples with an *N* under 15 are in parentheses.

The number of ribs seems not particularly closely correlated with either size or general sculpture. It is rather low (mean, 26-30) in the Cat and Gun Cay populations and high in C (up to 32, 35). Population P, which in color is somewhat intermediate between the North Cat Cay and the North Bimini (C) populations, has the intermediate values of 30.21 and 30.37 (P₁ and P₂). Only one (D) of the "smooth-shelled" populations has enough ribbed individuals to give a reliable figure. With a mean of 31.24 it is intermediate between the low rib number of the Cat Cay populations

and the high one of C. The two most pronounced hybrid populations, A (31.8) and N (28.2), likewise have intermediate figures, but N, as in other characters, is close to Cat Cay.

The variability is puzzling. It is highest ($C.V. = 10.7, 10.84$) in two otherwise very uniform populations from North Cat Cay (T, NCC), it is lowest ($C.V. = 7.16$) in a neighboring Cat Cay population (E), and is intermediate (8.74, 10.09) in the hybrid populations (A, N). This type of variability is at present inexplicable.

NUMBER OF WHORLS: The number of whorls does not vary nearly so much as one might expect on the basis of differences of length. It varies from 8 to 11.5, but is actually in nearly all adult specimens 9 or 10 (including the entire range from 9.0 to 10.9). The mean is slightly less than 9.5 in C, P₂, F, and A; between 9.5 and 10 in P₁, E, T, NCC, D, and W; and between 10.0 and 10.5 in N, H, B, and L. There is thus a slight average increase in the number of whorls with size (about one-half whorl per 4 mm. in length). The six populations with a mean shell length of less than 24.5 have 9.6 whorls or less, and the four populations with a shell length of more than 27.0 have mean whorl numbers of 9.98, 10.22, 10.29, and 10.40. The populations that are intermediate in shell size (24.5–26.5) are on the whole also intermediate in the number of whorls. The number of whorls shows little variability in adults of any one population but, as the determination of the exact number of flat embryonic whorls is somewhat subjective, too precise a statement of variation (e.g., calculation of the $C.V.$) would be meaningless.

COLORATION

An accurate classification and rating of color have proved impossible. Essentially two elements contribute to the coloration, an over-all ground color and a superimposed variegation pattern. The variegation is largely independent of the presence of pigment and appears as a "ghost" pattern in many shells of L that have little pigmentation. Pattern can be scored rather easily in smooth shells, but where ribs are well developed they seem to obscure the variegation, particularly where the ribs are paler than the background (most Cat Cay populations, also, in part, N, O, and W). Scoring the ground color is made difficult not only by the presence of ribs and the obvious bleaching of old individuals, but also because the color tone depends on two factors, density of the pigment and its coloration. Thus a shell may be paler than another one, either because it is bleached, or less pigmented, or colored by a paler pigment, e.g., yellow or pink, instead of walnut or red-brown.

No general discussion of color is given in this section for the stated reasons. It is included below with the detailed discussion of the taxonomic characters of the various colonies.

CHARACTERIZATION AND SYSTEMATIC ARRANGEMENT OF BIMINI *CERION* COLONIES

The facts presented in the preceding section offer the raw material for a classification of the Bimini colonies of *Cerion*. Two major questions must be answered: Are these colonies evenly distinct from one another, or can they be classified into well-defined groups? If definite groups can be distinguished, should they be considered full species?

It may be useful at this point to summarize in a few sentences the past taxonomic treatment of the Bimini *Cerion* (Clench, 1942). The names *cinereum*, *glans*, *incanum*, *maynardi*, and *pannosum* have been erroneously applied to specimens from the Bimini group, but the type localities of these species lie outside the Bimini area. Only five names have been based on populations from the Bimini area: *pillsburyi* Pillsbry and Vanatta (1898), *canonicum* Dall (1905), *northropi* Dall (1905), *biminiense* Henderson and Clapp (1913), and *lernerii* Clench (1956). The first three names were given to samples from Gun Cay, where only one single variable species occurs. The names *canonicum* and *northropi* are therefore correctly considered by Clench (1942) to be synonyms of *pillsburyi*. Specimens from D (North Bimini), A (South Bimini), North Cat Cay, and South Cat Cay have generally also been listed as *pillsburyi*.

A second species, *biminiense* Henderson and Clapp (1913), was recognized from the southern end of North Bimini (C) and from the southwest corner of South Bimini (P). Clench (1942) remarks that certain colonies show evidence of crossing between these two species.

Finally, a third form, *lernerii* Clench (1956) has recently been described and provides a name for the highly distinct entity of East Bimini (L).

The extensive information provided by the new collections shows that it is not possible to classify the existing colonies simply in terms of these three nominal species. Actually, topotypical "*pillsburyi*" (N) form a highly variable hybrid population (as does A). The remaining colonies can be classified in three groups:

The *lernerii* population group
The Cat Cay population group
The *biminiense* population group

Before an attempt is made to determine the taxonomic status of these population groups, it will be useful to describe the characters and the variability of each population, as indicated by the available samples.

MORPHOLOGICAL CHARACTERISTICS OF *CERION* COLONIES ON BIMINI

COLONIES OF THE *leneri* TYPE

All are distinguished by rather large size, rather cylindrical shape (low width/length index), generally smooth shell, white ground color, and

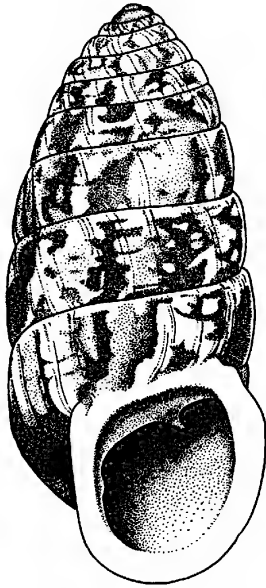


FIG. 6. Characteristic specimen of *leneri*.

strong variegation. The only "pure" colony of this type (L) is found near the southern tip of East Bimini. Other colonies of this group (B, H, D) give some indications of gene flow from *biminiense*.

COLONY L, TYPE COLONY OF *leneri*: Comparatively uniform in size, sculpture, and color. The greatest variation occurs with respect to the depth of pigmentation. The extent of variegation is rather similar in most of the 168 shells (including 20 immatures); however, it is distinctly brown in 51 (30.4%) shells, colorless (= "ghost") in 44 (26.2%) shells, and intermediate in 73 (43.4%) shells, in all cases on a whitish back-

ground. The pattern of the variegation is either very regular or more diffused and blotched. There does not appear to be any correlation between type of variegation and either shape or sculpture. Cylindrical and oval shells, very smooth and fairly costate types, occur among all three types of variegation. It is unknown to what extent the variation in this colony is affected by gene flow from Colony O. (For dimensions, proportions, and other numerical data, see table 6 and figures 2-7).

COLONY B: With the chief characteristics of the *lernerii* type. Differs



FIG. 7. Variation in *lernerii*.

slightly from typical *lernerii* (L) by being paler brown, by having the variegation less regular and less well defined, and by being more often costate and often almost pure white. The reduction of a well-pigmented variegation is perhaps the most characteristic feature of B (compared with L). In most of the characters in which this population deviates from L, it shows an approach towards *biminiense*. In the sample 20 (29.3%) snails are more or less white, 18 (26.5%) are distinctly variegated, and 30 (44.2%) have a more generalized suffusion of pale brown over the white ground color. These ratios are similar to those of the three types in L. (See table 6.)

COLONY D: Similar to B but very much whiter. In the sample there are 97 (62.5%) white shells, 47 (30.4%) whitish snails with slight variegation or a slight yellowish or brownish wash, and only 11 (7.1%) distinctly variegated snails which, however, are paler than the variegated snails of B. The shape is rather variable, but on the whole the shells are more oval and more rugged than those of B. There are a few excessively long shells in the sample (see table 6).

TABLE 6
STATISTICS OF POPULATION SAMPLES OF BIMINI *Cerion*

	<i>N</i>	Range	Mean	<i>S. E.</i>	<i>S. D.</i>
SAMPLE L					
Length	148	23.9 -31.9	27.76	0.12	1.47
Width	148	9.9 -12.7	11.26	0.04	0.54
W/L index	148	35.3 -46.3	40.59	0.20	2.39
Mouth	142	9.6 -12.6	10.91	0.05	0.59
Whorls	148	9.25-11.25	10.29	0.03	0.36
Ribs	2	26, 35	—	—	—
Sculpture	148	0.0 - 1.8	0.21	—	—
SAMPLE B					
Length	63	24.9 -32.4	28.98	0.19	1.54
Width	68	10.8 -12.6	11.59	0.05	0.45
W/L index	63	35.1 -45.6	40.11	0.32	2.52
Mouth	63	9.7 -11.9	10.87	0.07	0.54
Whorls	68	9.25-11.0	10.40	0.05	0.42
Ribs	5	28 -36	32.8	—	—
Sculpture	68	0.0 - 2.0	0.37	0.05	0.32
SAMPLE D					
Length	154	24.9 -34.9	29.41	0.15	1.80
Width	155	10.8 -13.5	12.17	0.04	0.49
W/L index	154	34.8 -50.0	41.50	0.20	2.49
Mouth	152	10.0 -12.9	11.25	0.05	0.57
Whorls	155	9.0 -11.50	9.98	0.03	0.44
Ribs	41	27.0 -37.0	31.24	0.43	2.74
Sculpture	155	0.0 - 3.2	0.83	0.04	0.51
SAMPLE H					
Length	14	22.1 -31.1	26.35	0.65	2.44
Width	16	10.1 -12.4	11.29	0.14	0.57
W/L index	14	37.3 -48.8	42.76	0.75	2.80
Mouth	14	9.0 -11.4	10.25	0.18	0.66
Whorls	16	9.0 -11.50	10.05	0.16	0.65
Ribs	—	—	—	—	—
Sculpture	16	0.0 - 2.1	0.59	—	—
SAMPLE T					
Length	107	20.9 -33.4	24.42	0.16	1.67
Width	110	8.9 -11.0	10.12	0.04	0.40
W/L index	109	32.0 -49.3	41.69	0.27	2.81
Mouth	107	8.0 -10.8	9.35	0.05	0.49
Whorls	110	8.5 -11.25	9.61	0.04	0.47
Ribs	110	24.0 -35.0	27.86	0.28	2.98
Sculpture	110	2.0 - 3.9	3.14	0.03	0.27

TABLE 6—(continued)

	<i>N</i>	Range	Mean	<i>S. E.</i>	<i>S. D.</i>
SAMPLE E					
Length	241	18.6 –29.1	24.61	0.10	1.62
Width	244	8.1 –11.3	9.97	0.03	0.50
W/L index	241	35.2 –47.8	40.62	0.15	2.30
Mouth	241	7.1 –11.2	9.37	0.04	0.55
Whorls	244	8.0 –11.25	9.87	0.03	0.44
Ribs	244	20.0 –35.0	26.80	0.12	1.92
Sculpture	244	1.5 – 4.0	3.06	0.03	0.52
SAMPLE NCC					
Length	69	21.2 –29.0	25.13	0.19	1.59
Width	72	8.9 –10.9	10.01	0.05	0.39
W/L index	69	34.4 –45.4	39.92	0.31	2.58
Mouth	69	8.1 –10.4	9.35	0.05	0.46
Whorls	72	9.0 –11.25	9.99	0.05	0.47
Ribs	72	21.0 –34.0	27.04	0.34	2.93
Sculpture	72	1.5 – 3.5	2.78	0.06	0.48
SAMPLE F					
Length	14	17.6 –25.8	21.34	0.56	2.10
Width	14	7.7 –10.1	8.93	0.20	0.74
W/L index	14	38.2 –44.2	41.96	0.49	1.83
Mouth	14	6.4 – 9.4	8.21	0.23	0.85
Whorls	14	8.75–10.0	9.37	0.11	0.40
Ribs	13	26.0 –36.0	30.23	0.76	2.74
Sculpture	14	0.0 – 3.8	2.83	—	—
SAMPLE S					
Length	82	21.0 –30.3	24.63	0.20	1.84
Width	83	9.0 –11.5	10.09	0.06	0.54
W/L index	82	35.8 –47.3	41.28	0.25	2.24
Mouth	82	8.0 –11.0	9.31	0.07	0.68
Whorls	83	9.0 –11.75	9.96	0.05	0.44
Ribs	79	19.0 –32.0	24.89	0.27	2.44
Sculpture	83	0.4 – 4.0	2.88	0.09	0.79
SAMPLE O					
Length	27	21.3 –27.6	25.20	0.29	1.50
Width	28	9.7 –11.1	10.48	0.07	0.35
W/L index	27	36.3 –46.8	41.78	0.45	2.34
Mouth	26	8.8 –10.4	9.79	0.07	0.38
Whorls	28	8.75–10.50	9.78	0.08	0.41
Ribs	14	24.0 –35.0	29.00	0.86	3.23
Sculpture	28	0.1 – 3.4	1.32	—	—

TABLE 6—(continued)

	<i>N</i>	Range	Mean	<i>S. E.</i>	<i>S. D.</i>
SAMPLE W					
Length	7	23.5–25.9	24.70	0.35	0.93
Width	8	9.5–10.6	10.26	0.13	0.38
W/L index	6	38.5–43.0	41.03	0.73	1.78
Mouth	6	8.8–10.4	9.57	0.23	0.57
Whorls	9	9.25–10.0	9.78	0.09	0.27
Ribs	8	24.0–31.0	26.75	0.77	2.19
Sculpture	8	1.4–3.8	2.68	—	—
SAMPLE P ₁					
Length	19	21.8–27.4	23.91	0.33	1.43
Width	19	9.3–10.9	10.34	0.10	0.42
W/L index	19	38.7–50.0	43.41	0.65	2.86
Mouth	18	8.4–10.3	9.65	0.14	0.59
Whorls	19	8.25–10.25	9.59	0.11	0.49
Ribs	19	27.0–36.0	30.36	0.52	2.29
Sculpture	19	3.50–4.0	3.94	0.04	0.17
SAMPLE P ₂					
Length	33	21.0–25.9	23.79	0.21	1.19
Width	34	9.5–11.1	10.2	0.06	0.36
W/L index	33	40.1–46.4	42.95	0.32	1.82
Mouth	33	8.5–10.9	9.4	0.09	0.52
Whorls	34	9.0–10.25	9.46	0.06	0.35
Ribs	34	26.0–37.0	31.20	0.41	2.42
Sculpture	34	3.0–4.0	3.69	0.05	0.30
SAMPLE C					
Length	95	20.6–27.8	23.39	0.15	1.46
Width	99	9.3–12.3	10.53	0.06	0.60
W/L index	95	39.6–52.5	45.03	0.27	2.68
Mouth	93	8.6–11.6	9.65	0.06	0.62
Whorls	99	9.0–10.50	9.49	0.10	1.03
Ribs	99	24.0–39.0	32.10	0.27	2.66
Sculpture	99	1.8–3.5	2.87	0.03	0.26
SAMPLE CB					
Length	67	20.3–27.8	24.25	0.21	1.73
Width	68	9.3–12.0	10.89	0.08	0.62
W/L index	67	41.0–52.0	45.00	0.26	2.17
Mouth	67	8.2–11.4	10.00	0.08	0.66
Whorls	68	8.50–10.25	9.33	0.04	0.37
Ribs	67	29.0–43.0	34.90	0.34	2.79
Sculpture	68	0.5–3.8	2.39	0.06	0.50

TABLE 6—(continued)

	<i>N</i>	Range	Mean	<i>S. E.</i>	<i>S. D.</i>
SAMPLE V					
Length	65	19.6 -27.7	23.48	0.20	1.62
Width	64	9.5 -12.3	10.91	0.07	0.55
W/L index	64	39.4 -52.4	46.61	0.36	2.85
Mouth	65	8.1 -11.2	9.81	0.07	0.61
Whorls	61	8.25-10.0	9.07	0.04	0.35
Ribs	—	—	—	—	—
Sculpture	—	—	—	—	—
SAMPLE A					
Length	279	21.8 -31.8	26.31	0.10	1.69
Width	280	10.0 -13.0	11.64	0.03	0.53
W/L index	279	36.4 -55.4	44.41	0.16	2.68
Mouth	279	9.1 -12.4	10.56	0.04	0.59
Whorls	280	8.0 -10.50	9.46	0.03	0.44
Ribs	208	26.0 -42.0	31.80	0.19	2.78
Sculpture	280	0.0 - 3.9	2.37	0.07	1.19
SAMPLE N					
Length	143	24.2 -32.0	27.78	0.12	1.46
Width	144	9.5 -12.1	10.92	0.04	0.47
W/L index	144	33.9 -46.3	39.41	0.19	2.22
Mouth	143	9.5 -11.9	10.48	0.04	0.48
Whorls	144	9.0 -11.25	10.22	0.03	0.41
Ribs	119	22.0 -37.0	28.24	0.26	2.85
Sculpture	144	0.3 - 4.0	2.88	0.09	1.13

SAMPLE H: The specimens collected as dead shells in the sand between B and D have lost all coloration. Size, proportion, and structure are recorded in various tables. This is a somewhat heterogeneous sample, not necessarily intermediate between B and D (see table 6).

COLONIES OF THE CAT CAY TYPE

Distinguished by small size and rather cylindrical or tapering shape. Well sculptured, but number of ribs per whorl low, variegation usually present but largely concealed by costation; ground color often brownish. As the hybrid population of Gun Cay (*pillsburyi*) is close to the Cat Cay type, the name *pillsburyi* may be used for this group of colonies.

COLONY T: This sample appears on first sight to be very uniform. However, on the basis of color, four classes of shells can be distinguished

among 111 specimens, as follows: pure white, 33 (29.7%); whitish with a partly brown ground color, 51 (46.0%); ribs still more or less whitish, but ground color solid brown (paler or darker), 20 (18.0%); shells brown with distinct variegation, seven (6.3%). In one or two specimens the ribs are almost as dark as the ground color, which is sometimes more earth-colored, sometimes paler (pinkish ocher). For sculpture, size, and proportions see table 6 and figures 2-5 and 8.

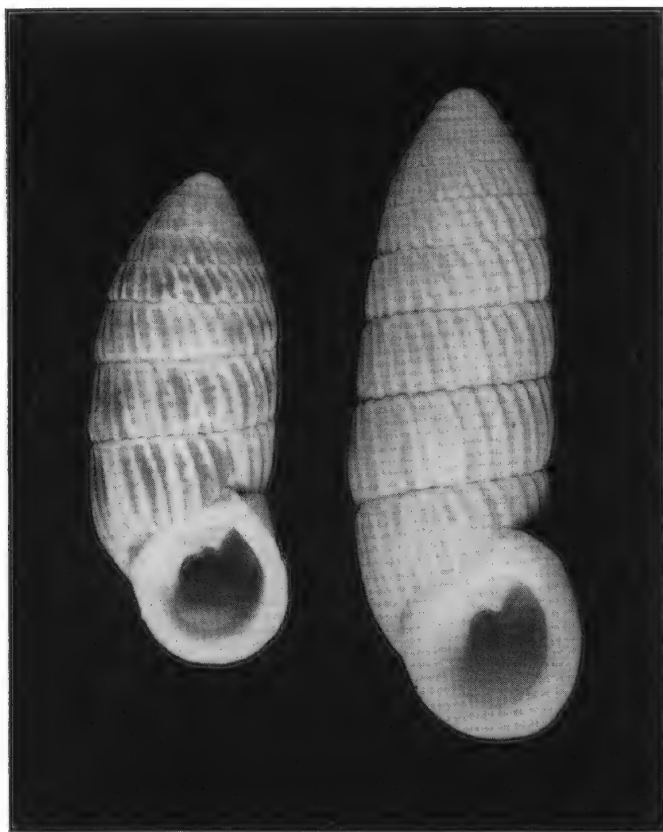


FIG. 8. Average-sized specimen (length, 24.6 mm.) and giant specimen (length, 33.4 mm.) from population sample T (North Cat Cay).

COLONY E: Very similar to Colony T but lighter. Forty (16.4%) specimens are pure white, 131 (53.7%) are almost white but shell with a slight suffusion of brown, and 72 (29.6%) more distinctly pigmented. Of the latter three or four (1.6%) appear variegated. Although the depth of pigmentation is less than in T, what little pigment there is seems to be consistently darker. The brownish tones prevail over the yellowish pink ones. Sculpture and shape seem remarkably uniform (see table 6).

COLONY NCC: For comparison, the measurements of sample NCC are also given (table 6).

COLONY F: Except for size quite similar to T, perhaps paler. Remarkable is a single, completely smooth white specimen. These are the smallest *Cerion* in the Bimini group (table 6).

COLONY S: Quite similar to T (North Cat Cay), but without any signs of variegation and of darker color. Generally the color tends to be more uniform, with the ribs in dark specimens not so conspicuous as in T. Four of the 91 shells are of the more or less smooth type. This includes a whitish and the darkest individual. The sculpture is coarse, with the ribs widely spaced.

Among 91 snails 26 are white or whitish, 41 are pale brown (to varying degrees of darkness), and 24 are dark brown. Most of the latter are darker than any shell in samples E and T. South Cat Cay specimens lacking variegation somewhat resemble P but differ from P in their more cylindrical shape, by having fewer ribs, a darker, duller coloration, and by their much greater range of variation (table 6).

INTERMEDIATE TYPES

The northern half of East Bimini is occupied by populations (O, W) that are so nearly intermediate between the *lernerii* and the Cat Cay type that they could be associated with either. In size, number of ribs, and sculpture they go with Cat Cay, in variegation they are near L. Their low variability indicates that they are not "hybrid" populations. They are located between two colonies of the *lernerii* type (L and B).

COLONY O: Clearly variegated in spite of the rather well-developed ribbing. Among 34 specimens the variegation is dark in nine (26.4%), intermediate in 15 (44.1%), and light (often "ghost") in 10 (29.4%). The sculpture rating of 1.32 ± 0.16 is much lower than in any Cat Cay population. Some specimens are almost smooth. There is reason to assume that the populations from L through O to W are continuous (table 6).

COLONY W: Still one step further removed from L. Very similar to O, but still smaller and with more regular costation. Individual shells not very different from variegated individuals from North Cat Cay (table 6).

COLONIES OF THE *biminiense* TYPE

Populations of this type are superficially similar to those of the Cat Cay type, but differ by uniform coloration, absence of variegation and polymorphism, smaller size, more oval and robust shape (higher width/length index), and higher number of ribs per whorl.

COLONY P_1 : On the whole, P_1 specimens are rather similar to Cat Cay snails, but differ in size, proportion, and absence of polymorphism. They are more strongly and more uniformly pigmented, the color being paler brown, more pinkish ocher. There are no white or whitish individuals (table 6).

COLONY P_2 : Specimens of P_2 are in appearance not diagnostically different from those of P_1 , averaging perhaps a little deeper in color and with the ribs contrasting less with the ground color of the shell (table 6).

COLONY C: These specimens are quite similar to P in robustness and in the absence of evident polymorphism in coloration. They differ from P by averaging even more bulbous (less cylindrical) and by the lighter and more pinkish clay, less brownish, coloration (table 6).

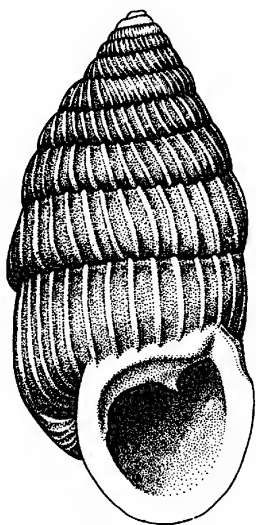


FIG. 9. Characteristic specimen of *biminiense*.

Included here are also the data of sample CB, collected near the type locality of *biminiense* (table 6).

In Colony C six dead shells were found which were occupied by hermit crabs and which differed so clearly from living C specimens that it was evident that they had been "imported" by the crabs. They are intermediate between C and V in size, sculpture, and coloration. The whiteness and absence of sculpture in some of these shells are strikingly different from anything found in C. In costation and whiteness these shells resemble V quite closely, but in size they are near the large extreme of V. Perhaps only the largest V shells are suitable for occupation by hermit crabs.

COLONY V: This subfossil colony is of special interest because it comes

from the wide gap between the very different populations C and D. *Cerion* is now extinct in this area, and the question arises as to whether this area was formerly occupied by a C-like or by a D-like population? An analysis of the sample reveals the extraordinarily interesting fact that the population was intermediate. In sculpture it is closer to D. Among 67 classified shells, only three are distinctly costate (although some of the smoothness may be due to post-mortem loss of costation). In size and general form, however, they are very similar to sample C. Color is not preserved in most of the shells. Where it is, it seems to be a uniform yellowish brown, without indication of a pattern of variegation. Together with the six shells inhabited by hermit crabs that were found in Colony C, which presumably came from the same population, these specimens give a good picture of the appearance of the extinct V colony (table 6).

"HYBRID" COLONIES

All colonies of *Cerion* show a certain degree of variability in size, proportion, sculpture, and coloration. Yet, at first sight, any sample from most of these colonies seems to be quite uniform. This is equally true for colonies of the *lernerii* type (as L or B), of the Cat Cay type (as E or T), and of the *biminiense* type (as P or C). This is in strong contrast to the appearance of two colonies (A, N) in the Bimini group that are characterized by a bewildering variability in color and sculpture. It is undoubtedly the appearance of these two colonies that led Clench (1942) to the statement that certain colonies show evidence of crossing between the two species *pillsburyi* and *biminiense*.

COLONY A: White is the prevailing color of this South Bimini colony, but all shells that are not pure white show variegation to a varying degree. A large sample was divided into five classes: (a) pure white, (b) faint coloring or some slight brownish streaking, particularly on the last whorl, (c) some brown between the ribs, even at the upper whorls, (d) brown more extensive, and (e) variegation conspicuous. The classes were represented among 241 shells as follows: a = 88 (36.6%), b = 94 (39.0%), c = 35 (14.5%), d = 15 (6.2%), e = 9 (3.7%). In a different sample, the figures were: a = 11 (28.9%), b = 14 (36.9%), c = 5 (13.1%), d = 6 (15.8%), e = 2 (5.3%). It is evident that in each sample the essentially white shells (a, b) comprise about two-thirds of the sample. In this respect the shells resemble somewhat those of D and B, or E and T, not those of the two adjacent colonies, P and C, which are always pigmented. On the other hand, in shape and sculpture many of the shells are indistinguishable from those in P or C. There is a rough correlation between sculpture and coloration. Among the 88 pure white shells there are 48

"smooth" ones (ribs can be counted not at all or only with difficulty), among the 35 (c) shells there is only one that is smooth, among 15 (d) shells none are smooth, and among the nine variegated shells five are smooth. Thus among the shells that are white or heavily variegated 55 per cent are smooth, while nearly all the more evenly colored shells are costate. Likewise there is correlation between size on one hand and ribbing on the other. The pure white smooth shells are larger than the heavily ribbed, well-pigmented shells. Indications are thus that the mixing of the two gene complexes is not complete and that the three characters (smooth shell, whiteness or variegation, and large size) tend to go together, as do costate shells, even brown color, and small shell. The parental forms thus reconstructed resemble a *lernerii* type (such as D) and a Cat Cay type (such as E).

Equally as remarkable as the variability in color and structure is the relative uniformity in size. The coefficients of variability for length (6.42), width (4.55), and relative width (6.03) of A are not appreciably larger than those of many "pure" colonies (table 6).

One of the most puzzling aspects of A is its location between Colonies P and C, both of the *biminiense* type, in the south and north. If one of the parental strains of A were something like E (with its great polymorphism of color) the variability of A would be more easily understood. Its location between the very uniform (and similar to each other) Colonies P and C is an unsolved riddle.

COLONY N: The population from Gun Cay represented by sample N likewise shows an amount of variability that is strong evidence for hybridization. When the shells are classified into ribbed and smooth and into four grades of pigmentation, the frequencies in the eight classes are as follows (percentages in parentheses) :

PIGMENTATION	RIBBED	SMOOTH	TOTAL
Absent	9 (5.3%)	4 (2.3%)	13 (7.6%)
Slight	28 (16.5%)	3 (1.8%)	31 (18.3%)
Medium	84 (49.4%)	15 (8.8%)	99 (58.2%)
Strong	18 (10.6%)	9 (5.3%)	27 (15.9%)
Total	139 (81.8%)	31 (18.2%)	170 (100.0%)

Thus about 18 per cent are smooth and 8 per cent white. The ratio of smooth to ribbed is roughly similar in all four pigment classes. The coloring is laid down in a variegated pattern, rather than being uniform. This is more easily seen in the smooth than in the ribbed shells.

Colony N resembles the colonies of the Cat Cay type in many respects, as, for instance, in the density of ribbing. Yet many differences are ap-

parent when N is compared with a specific colony. For instance no shells are found in T that are comparable to the more heavily pigmented types of N, although many of the lightly and medium-pigmented specimens of N match similar individuals of T quite well. The darkest N are also more heavily variegated; in fact some of them resemble L quite closely. The percentage of whites in N is lower and the size larger than in T. Variability in degree of costation is very high (table 6).

Although hybridization is not quite so obvious in N as it is in A, it is nevertheless the most likely explanation for the high variability of the Gun Cay population.

FORMAL CLASSIFICATION OF THE BIMINI *CERION*

If the extreme populations of Bimini *Cerion* are compared, *lernerii* (L) and *biminiense* (C), then it certainly seems justifiable to consider them valid species. They differ in a number of striking characters (table 7).

TABLE 7
PRINCIPAL SHELL CHARACTERS OF *lernerii* AND *biminiense*

	Length	Sculpture	Ground Color	Variegation	Shape
<i>lernerii</i>	Long	Smooth	White	Strong	Cylindrical
<i>biminiense</i>	Short	Heavily ribbed	Yellow-brown	Absent	Oval

Two important facts, however, militate against the recognition of these two forms as full species: the presence of intermediate populations and the occurrence of hybrid populations.

INTERMEDIATE POPULATIONS

There is an almost unbroken chain of intermediate forms between the two extremes. The morphological chains involved are not necessarily geographical chains, but are so in part:

L, O-W, T-P-C
L-B-D, V-C

Slight breaks in these chains are indicated by commas.

The intermediacy of some colonies is quite remarkable. For instance, O and W are in variegation and locality close to *lernerii* (L), but in size and sculpture closer to the Cat Cay group. V belongs in shape to *biminiense*; in fact it is even more extremely oval, yet in sculpture it trends

towards D, and the V-like individuals inhabited by hermit crabs suggest that there might even have been a reduction in color. The morphological chain O-T-P-C is unbroken. D still belongs to the L group; in fact its mean size is greater than that of any other population, yet in reduction of variegation and increase of sculpture it indicates a definite trend to *biminiense* (sample C). The Cat Cay populations, finally, are so clearly intermediate in several characters that they can be considered closer either to *biminiense* (sculpture, size) or to *leneri* (cylindrical shape, indication of variegation, paling of ground color). If one were to treat *leneri* and *biminiense* as two species, it would be virtually impossible to decide with which of the two species to associate some of the intermediate populations.

"HYBRID" POPULATIONS

The conspecificity of the forms ranging from *leneri* through Cat Cay to *biminiense* is furthermore supported by the existence of two hybrid populations. In these populations, one from South Bimini (A), the other from Gun Cay (N), a bewildering amount of variability is found. On Gun Cay specimens can be found that almost match specimens of the *leneri* type (L); others, the Cat Cay or the *biminiense* type. Likewise, on South Bimini, the individuals within a single colony (A) combine characters normally segregated in different colonies.

THE NAME OF THE BIMINI SPECIES

It is quite impossible to reach final conclusions on the taxonomy of the Bimini *Cerion* without taking the *Cerion* populations of other islands into consideration. There is great similarity between some of the Bimini populations and populations of *Cerion* that occur in other parts of the range of the genus. Smooth, heavily variegated shells, such as *leneri* (L), occur on Eleuthera and Cat Island (*eximium*), Little Cayman (*laevigatum*), Cuba (*torrei*, *sagraianum*, *politum*), New Providence (*gubernatorium*), Rum Cay (*lentiginosum*), Fortune Island (*marmoratum*), and Key West (*incanum fasciatum*). Populations similar to *biminiense* or the Cat Cay populations occur almost throughout the range of the genus. It is evident, then, that the Bimini populations cannot be definitely assigned to a species until the genus *Cerion* has been revised as a whole.

We have thus the paradoxical situation that colonies 500 kilometers distant are exceedingly similar while adjacent colonies, such as O and L or P and A, are quite different. Yet where such different types come in contact, they interbreed freely. In view of this failure of external characteristics in helping to define clear-cut species in *Cerion*, it has been sug-

gested that the internal anatomy might be more helpful. Unfortunately this is not necessarily the case. Bartsch (1920) reports anatomical differences between individuals of several species of *Cerion*, but these differences are not nearly so clear cut as is the case in many other genera of mollusks. Nor is anything said on the number of specimens dissected. This is important in view of Jaenicke's (1933) findings that there is considerable individual variation in the number of radula teeth, the form of the jaw, and the absolute and relative length of the various parts of the genital tracts and accessory structures. He was unable to discover decisive differences between various forms of *Cerion glans*, *exumense*, and *vannostrandii*. On the other hand, there were well-defined differences between *C. glans* and *C. uva* (Jaenicke, *op. cit.*, p. 369).

TAXONOMIC DESIGNATION OF VARIOUS COLONIES

Taxonomic entities below the species level are customarily designated as subspecies. "Subspecies are geographically defined aggregates of local populations which differ taxonomically from other such subdivisions of a species" (Mayr, Linsley, and Usinger, 1953).

Some taxonomists ask for no other criterion, in order to recognize a subspecies, than demonstration of a statistically significant difference of the means of certain characters. If one were to accept such a standard one would have to recognize nearly every *Cerion* colony in the Bimini group as a separate subspecies. This is clearly true for L, O, B, D, V, C, A, P, N, E, and F. A handful of specimens of any of these 11 colonies can be identified at sight. The differences between other colonies are less striking.

Colony W does not show statistically significant differences from O in any dimensional characters (although a larger sample might), but, as shown in table 4 and figure 5, there is a considerable difference in sculpture. About half of O are more or less smooth, while all of W are ribbed.

Colony E is similar to T in most characters, but there are slight differences between the means for width, number of whorls, and number of ribs, in addition to the slight color differences described above.

The difference between P_1 and P_2 is apparently not significant for any of the measurable characters. The same is true for most measurable differences between C and P_1 , except that the greater number of ribs of C is almost significant and the heavier sculpture of P_1 is definitely so (table 4 and fig. 5). There is also an average color difference, as described above. In spite of these slight differences there are a number of samples such as P_1 and P_2 , or E and T, which are not unambiguously distinguishable. Colonies P_1 and P_2 are perhaps in contact with each other, and on North Cat

Cay E and T are merely samples drawn from a continuous dense population, taken a few hundred yards apart, while F is that part of this same array of populations that has entered woodlands. It would hardly seem helpful to call each a separate subspecies. On East Bimini it seems that L changes within about 2 miles into O; there is probably a continuity of populations (although the intervening area has not yet been sampled).

More confusing than the continuity of populations is the irregularity of their distribution (see fig. 1). The population of the *lernerii* type on East Bimini (L) is separated from populations on North Bimini (B, D) by two populations (O, W) somewhat resembling the Cat Cay type. *Cerion biminense* (C) of North Bimini is separated from the very similar population (P) at the south tip of South Bimini by the very different hybrid population A.

Finally, there is reason to believe that some of the populations may have closer relatives on other islands than in the Bimini group (e.g., *lernerii* on Eleuthera and Cat Island; Clench, 1956).

For all these reasons, it would seem preferable at the present time to refrain from introducing a lot of new subspecific names. For the two extremes we use the scientific designation *biminense* and *lernerii*. The name *pillsburyi* is available for the hybrid population on Gun Cay and for the Cat Cay type which is not very different. All other colonies are best designated by the combination of a group name ("*biminense*," "*lernerii*") and a colony letter (B, D, P) or by island and colony letter.

DISCUSSION

It is necessary for a complete understanding of the processes of evolution to study a great variety of animals and plants. The data presented in the preceding sections indicate that population structure in the snails of the genus *Cerion* is fundamentally different from that of a species of bird or pelagic marine invertebrate. Even though the genetics of *Cerion* have not yet been studied (and probably never will be) as was done by Rensch (1937) for *Murella*, it is possible to draw various conclusions on evolution and speciation on the basis of the presented data. In order to facilitate the analysis a summary is presented of the observed phenomena.

1. Only one species of *Cerion* is found in the Bimini group at any one place.

2. The snails live semi-colonially, high population densities occurring locally, there being no evidence of any spacing due to territoriality.

3. All colonies show considerable phenotypic variability. Polymorphism in size, proportions, coloration, and sculpture is frequent even in "pure" colonies. Curves of variation are frequently bimodal.

4. Variability is greatly increased in certain colonies, designated as "hybrid" colonies.

5. The number of variable characters is considerable. Size, shape, color, and sculpture are known to be affected by variation. Variation in the internal anatomy and physiology were not studied.

6. Various characters may assort independently, in the variable populations as well as in the intermediate populations. For instance, population O has the coloration of *lernerii* but size and sculpture of the Cat Cay group.

7. There is extreme geographic variation. No two colonies are identical, and sometimes even contiguous populations are clearly distinguishable, such as L, O, W, and the Cat Cay populations E and F.

8. The distribution of the various colonies is irregular. Very similar colonies are sometimes separated by very different ones. For instance, the rather similar Colonies L and B of the *lernerii* group are separated from each other by O and W which in several features are more similar to the colonies on rather distant North Cat Cay. The exceedingly similar Colonies C and P are separated from each other by the very different hybrid population A.

9. Wherever two populations are in contact with each other there is evidence of gene flow. In some cases there seem to be regular clines, as between O and W or between E, T, and F. A cline probably also exists between L and O but remains to be substantiated by further collecting. Subfossil material indicates that clines may also have existed formerly between B and D and between C, V, and D. Extermination of the connecting populations has disrupted these clines.

10. There is no evident correlation between phenotype and occupied habitat (table 2). The small size of F is the only character that suggests a direct correlation between phenotype and environment. Woods are on the whole a habitat unsuitable for this species.

The stated facts raise a number of questions which are of considerable biological significance.

STABILITY OF THE PHENOTYPE

The first question is to what extent the differences between populations have a genetic basis, or reciprocally to what extent the phenotype of a colony is modified by the effects of the local environment.

The assumption that the greater portion of the phenotypic differences between colonies of *Cerion* has a genetic basis is supported (a) by the fact that very different phenotypes occur in close neighborhood in essentially identical environments, such as L and O on East Bimini, D and C

on North Bimini, A and P on South Bimini; (b) by the fact that divergent phenotypes co-exist in the hybrid colonies; (c) by analogy with the work of Goldschmidt, Sumner, and other population geneticists who have studied genetic differences of natural populations; and (d) by the transplantation experiments of Bartsch (1920-1929) who reports that the descendants of *Cerion* transplanted from the West Indies to the Dry Tortugas were still indistinguishable from the parentals after several generations.

PATTERN OF DISTRIBUTION

The "crazy-quilt" pattern of distribution of West Indian *Cerion* poses a real problem. The analysis indicates that it is the result of contradictory capacities for dispersal. The extreme localization of many colonies and the relatively great difference of neighboring colonies indicate very low dispersal. The horizontal movement of a snail may not exceed a few meters in a lifetime. The young snails remain presumably near their place of birth. This tendency for extreme sedentariness in *Cerion* is compensated by a capacity for occasional long-distance dispersal during hurricanes. The result of this capacity is irregular distribution, the possibility of multiple invasions of the same island, the establishment of a checkerboard pattern of distribution, and extensive hybridization of types secondarily brought into contact with one another.

Owing to the devastating effects of hurricanes and fires there is presumably a steady extermination of colonies. The vacant habitats are recolonized by founder individuals. In view of the fact that these snails are hermaphrodites it is possible and probable that many if not most colonies are founded by a single fertilized adult. Two factors tend to promote rapid divergence of such colonies. Comparatively high inbreeding among the early generations derived from the founder individual exposes homozygous genotypes more often to selection than in outbred populations. Also the impact of the new environment may lead to a drastic modification of the contents of the gene pool in the new population and consequently in the phenotype (Mayr, 1954).

Each new colony is an evolutionary experiment. The eventual fate of such a colony is indeterminate. It will either become extinct before having made contact with adjacent colonies or undergo some gene exchange or even complete fusion.

On the island with the greatest population density (North Cat Cay), the snails show the greatest ecological tolerance (table 2). In other areas of locally high population density (D, L, A) the ecological tolerance is not nearly so great.

HYBRIDIZATION AND ITS EFFECTS

Hybridization is usually defined as the interbreeding of two different "kinds" of animals or plants. There has been a recent tendency to equate "kind" with "species" and thus give hybridization a biological meaning. Laudable as this endeavor is (or else one may have to call, with Lotsy, all sexual reproduction hybridization), it leads to difficulties in a genus such as *Cerion* where it is so difficult to delimit species. Hybridization here may be applied to all situations where populations interbreed which belong to very different morphological types.

In the Bimini group such hybridization occurs whenever two different types of *Cerion* come into contact. The evidence for this comes from character clines, such as C-V-D-B or L-O-W, or from "hybrid" colonies, such as A and N, which are characterized by high variability in sculpture and coloration and an essentially independent assortment of characters. There is no evidence for anything but random mating in these hybrid colonies. On the other hand, the segregation of the characters is not entirely independent. As described (p. 37), among shells of the *lernerii* color type in Colony A, 55 per cent are smooth, while nearly all shells of the Cat Cay color type (rather evenly pigmented) in this colony are costate. There is a tendency for three characters to go together: smooth shell, whiteness (with or without well-defined variegation), and large size, versus costate shells, even brown color, and small size. This long-continued hanging together of parental characters in hybrid populations has been stressed particularly by Anderson. It is not nearly so evident in population N as it is in A. Large population size in itself does not greatly affect variability. The exceedingly populous and extensive populations of *Cerion* on North Cat Cay are no more variable than most small isolated colonies.

REPRODUCTIVE ISOLATION

The readiness with which colonies of the *biminiense*, Cat Cay, and *lernerii* types hybridize with one another, in spite of the pronounced morphological differences, suggests that reproductive isolation is not easily acquired in this genus. This is supported by Bartsch's (1920) experiment, in which the introduction of *Cerion viaregis* on Newfound Harbor Key resulted apparently in free hybridization with the native species *C. incanum*. On the other hand, there are some localities within the range of *Cerion* where two (or perhaps even more) species of *Cerion* coexist sympatrically, which indicates that isolating mechanisms of at least a certain degree of efficiency had evolved. Bartsch (1920) reports that on Loggerhead Key the two introduced species, *C. casablancae* and

C. viaregis, continued to coexist without interbreeding. There is no predictable correlation between degree of difference in shell characters (except possibly size!) and sexual isolation. To what extent differences in the internal anatomy may give clues on the degree of sexual isolation has not yet been studied thoroughly.

CONCLUSION

The genus *Cerion* offers the picture of an actively speciating group, eminently capable of rapidly filling vacant niches in its peculiar specialized habitat. Morphological differences are rapidly acquired, but isolating mechanisms evolve only slowly. Great plasticity is maintained by the steady extermination of populations and reestablishment of new ones. Isolation appears temporary, to be followed subsequently by the fusion of populations. These characteristics make the genus eminently well adapted for the pioneer habitat in which it lives and which changes continuously as a result of shifts in sea level (submergence and fusion of islands), changes in the plant cover, or destruction by hurricanes and fire.

Cerion appears to be an extreme example of reticulate evolution on the infraspecific level. The very characteristics, however, which have adapted these snails so superbly for the habitat in which they live make it virtually impossible to classify them in terms of the conventional categories of species and subspecies.

SUMMARY

1. A survey was made of the *Cerion* snails in the Bimini group, Bahama Islands. Samples were obtained of every colony on North, East, and South Bimini, and the location and extent of the colonies were mapped. Samples from Gun Cay, North Cat Cay, and South Cat Cay were also studied. Subfossil dead shells of *Cerion* were collected in several areas where *Cerion* has become extinct.

2. Each colony has its own diagnostic characteristics of size, shape, sculpture, and coloration, but three groups of colonies are distinguishable: the *lernerii* group, the *biminiense* group, and the Cat Cay group (*pillsburyi*). Even though superficially each group appears to be a separate species, each is allopatric, and adjacent colonies show signs of gene exchange. Two colonies are apparently hybrid populations.

3. Hybrid colonies show high variability (*C.V.*) with respect to sculpture (amount of costation) and coloration, but size and shape are not more variable than in other colonies.

4. Colony size is very variable, ranging from a few hundred individuals to several hundred thousands.

5. Some colonies are isolated from one another by stretches of from 1 to 5 kilometers of unsuitable or unoccupied terrain; in other areas the colonies form an uninterrupted band parallel to the beach.

6. The colonies are similar to one another in basic ecology, but differ in preference for substrate (coral rock or sand), preferred plants, and exposure.

7. Geographic variation is pronounced, but irregular. The facts are best explained by one's assuming two antagonistic tendencies: a high degree of sedentariness and infrequent long-distance dispersal by hurricanes.

8. Differences in shell characteristics evolve more rapidly than reproductive isolation. As a consequence, some populations which had become morphologically very distinct during a period of isolation were still able to interbreed freely when they again came into contact.

9. The characteristics that adapt *Cerion* so superbly to its continuously changing habitat make it exceedingly difficult to classify the populations of this genus in the conventional categories of species and subspecies.

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